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Notes on Certain Primitive Heterodont Pelecypods

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Bernard's important studies on the development of the pelecypod hinge (Bernard, 1895, 1898) led him to certain general conclusions regarding phylogeny in the class. Although he was perhaps overly influenced by Haeckel's recapitulation theory, so popular in his day, some of his conclusions about phylogeny are still valid as tested by the evidence of stratigraphic sequence. Many are yet to be assessed.

He noted that in the most advanced, or heterodont, hinge, anterior and posterior pairs of lamellae ("primitive lamellae") become differentiated during growth into two stable marginal series, which he termed the anterior and posterior laterals, and an intermediate group beneath the beaks, the cardinals. He showed that the cardinals are modified portions of the anterior laterals. Development of the posterior laterals seems to be somewhat independent of the other teeth. The heterodonts were so defined by Bernard in terms of this characteristic ontogenetic development of the hinge.

Several true heterodonts are found in Devonian and even older strata, but there is uncertainty about the exact time and nature of the derivation of the heterodont hinge. Bernard, who did not live to complete his studies, found some evidence of polyphyletic origin of the heterodonts in diverse Ordovician ancestors, Modiolopsidae, Pterineidae, and the cyrtodonts (Bernard, 1898).

Some of the early Paleozoic forms alluded to and also some modern forms (e.g., unionaceans) resemble heterodonts in the possession of elongate posterior dorsal teeth, and a few small teeth beneath the beak. They do not generally, however, possess anterior lateral teeth. They

differ from heterodonts in the posterior part of the hinge. The posterior teeth extend backward from the beaks beneath the ligament. They are not clearly separated from the cardinal series by the ligament as in modern heterodonts. The dental patterns in these forms are much more variable than those of the heterodonts, and the unionaceans, at least, possess nacreous rather than crossed-lamellar structure characteristic of the heterodonts.

Bernard (*op. cit.*) regarded the posterior teeth of unionaceans and Paleozoic modiopsids, pterineids, parallelodonts, and certain others as undifferentiated "primary lamellae." Later authors have variously termed these teeth posterior cardinals, pseudo-cardinals, and pseudo-laterals in an attempt to distinguish them from the laterals of heterodonts. Others have designated the elongate posterior teeth as "posterior laterals" on the grounds that they probably are actually homologous with those of heterodonts. This is the usage adopted here. Douvillé (1913) applied the term actinodont to those primitive forms in which the dorsal lamellar teeth extend beneath the ligament to the beak region. Many of the early Paleozoic families were grouped together by him in a general category defined by possession of this actinodont dentition. The modern unionaceans he regarded as actinodonts structurally trending towards the hinge condition of the heterodonts.

The earliest known pelecypods that possess differentiated posterior lateral teeth are mid-Ordovician genera referred provisionally here to the Modiopsidae (P. Fischer, 1887, p. 989 = Modiopsidae Ulrich, 1894). Unfortunately, not any of the Ordovician genera are really well known. Ulrich (1894) has described hinge characters in a number of these early shells from specimens that unfortunately are quite fragmentary (fig. 1). It is claimed, but not satisfactorily demonstrated, that *Modiopsis* lacks posterior laterals. These and related shells are more

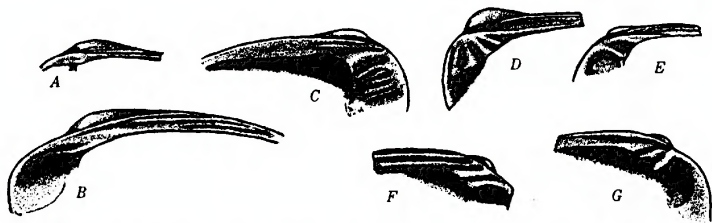


FIG. 1. Lower Paleozoic Modiopsidae. A. *Modiopsis versailensis* Miller, Cincinnati. B. *Modiopsis valida* Ulrich, Cincinnati. C. *Modiomorpha concentrica* Conrad, Hamiltonian. D. *Modiolodon ganti* (Safford), Trentonian. E, F. *Modiolodon winchelli* (Safford), Trentonian. G. *Modiolodon oviformis* Ulrich, Trentonian. All figures $\times 1$. After Ulrich, 1894.

or less elongate, with short anterior extremities and forward-directed beaks. Correlated with these characteristics, the ligament is external, opisthodontic, and elongate. The hinge teeth consist of a few small cardinal teeth that tend to be radially disposed with respect to the beaks. The Devonian genus *Modiomorpha* possesses several elongate posterior hinge teeth parallel to the margin of the hinge. *Redonia* from the Ordovician of Brix, probably a modiolopsid, possesses one elongate posterior lateral tooth in each valve. These extend from the posterior extremity of the hinge to the beaks (Douvillé, 1913, p. 441, figs. 14, 15). A similar Ordovician form, *Actinodonta acuta*, from the same locality also possesses well-defined posterior laterals (*op. cit.*).

A characteristic of the majority of the modiolopsids is a more or less elevated ridge, or myophoric buttress, immediately behind the anterior adductor impression. Generally the shells are unornamented or occasionally marked by concentric ridges, or in some cases by radial, usually weak, ribs which extend over the posterior three-quarters of the shell.

There are several genera in the late Paleozoic remindful of early Paleozoic modiolopsids. These are distinguished from the older forms by a reduction in the number of cardinal teeth and by the separation of the lateral teeth from the beaks, the latter becoming restricted to the posterior portion of the hinge as with true heterodonts. Examples of this group are *Stutchburia*, *Netschajewia*, and *Myoconcha* (= *Labayaphorus*) (fig. 2A-D). These are Permian forms, and the last-named genus ranges well into the Mesozoic. They are sufficiently compact and distinct from other groups of pelecypods that I am proposing a new family for them, the Myoconchidae. In all these shells the upper postero-lateral tooth of the right valve lies above a corresponding tooth of the left valve, a relationship known in certain other heterodonts but nevertheless somewhat unusual. The left valve contains a single, rather prominent, postero-lateral tooth which is separated from the margin of the valve by a well-defined furrow for the reception of the marginal tooth of the right valve. A low, marginal, postero-lateral tooth occurs in the right valve, and in some cases this overlies an obscure inner tooth (fig. 2C-D).

There may be a single cardinal tooth in each valve, but this is poorly developed in some shells, and it may be lacking entirely in left valves (*Myoconcha*).

Modiolopsidae (and *Myoconcha*) have been classed by many students as Mytilacea because of a tendency for reduction of the anterior adductor and the pedal lobe so that the beaks become progressively

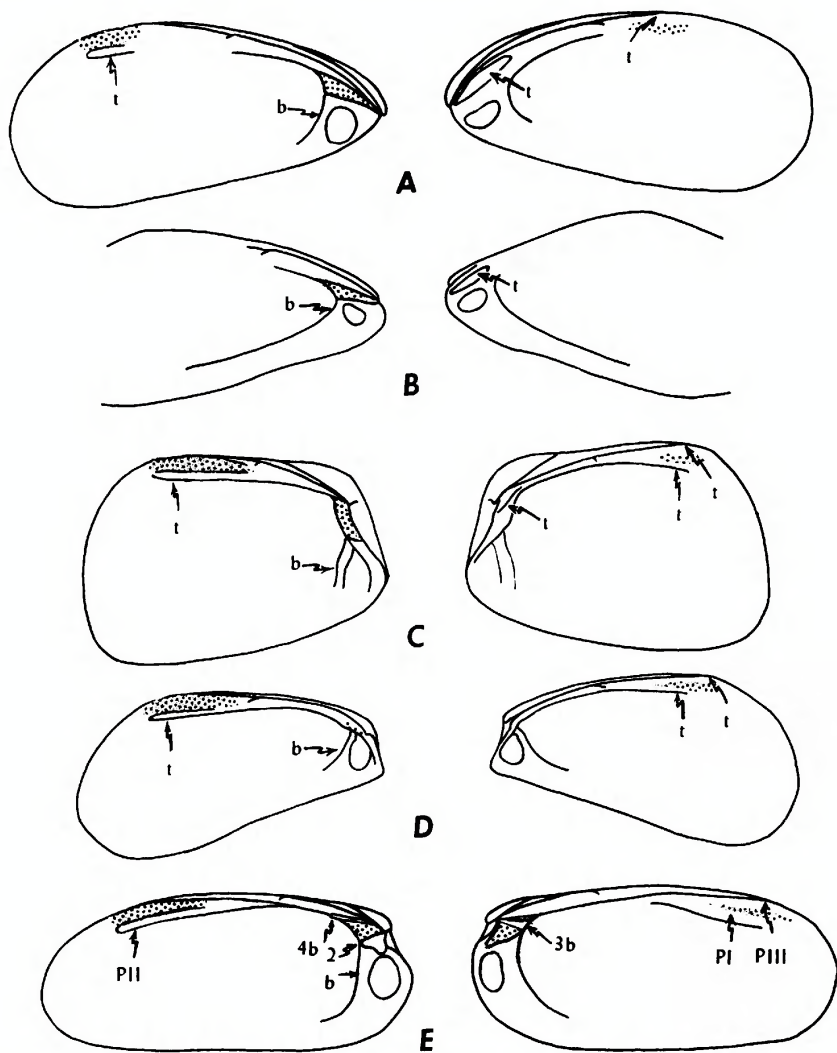


FIG. 2. Diagrams of primitive carditaceans and modiolopsids. A. *Myoconcha crassa* Sowerby, Jurassic, $\times \frac{1}{2}$. B. *Labayaphorus magnus* Licharew, Permian, $\times \frac{1}{2}$. C. *Rimmyjimina arcula* Chronic, Permian, $\times 5$. D. *Netschajewia* cf. *modioliformis* (King), Permian, $\times 2$. E. *Pleurophorus albequus* Beede, Permian, $\times 2$. Myophoric buttress indicated by letter b, teeth by t, or by numerals. Sockets are stippled.

anterior in position. The hinge characters and general expression of *Myoconcha* are remindful of the carditid *Beguina* Röding.

The general form, ornamentation, the highly characteristic arrange-

ment of the postero-lateral teeth, the ligament nymphs, and the anterior myophoric buttress characteristic of myoconchids also occur in other forms, *Permophorus* Chavan (= *Pleurophorus* King), and the early Mesozoic genera *Triaphorus* Marwick and *Kalentera* Marwick. Chavan (1954) has shown that these three genera most probably are members of the Carditacea.

The classification of teeth in the most complete hinge of *Permophorus* known to me follows Chavan's interpretation (fig. 2E). In a large series of well-preserved silicified Permian representatives of *Permophorus* I have been unable, however, definitely to recognize cardinal tooth 3a. Tooth 4b occurs in a number of specimens, but in other equally well-preserved shells it seems to be missing completely. Likewise, there are shells in which tooth PI does not develop.

Permophorus provides clues for the interpretation of the hinge of *Myoconcha*. By analogy it would seem that the single postero-lateral tooth of the left valve of *Myoconcha* and its relatives should be designated PII. The marginal postero-lateral tooth of the right valve then would be PIII (fig. 2A, C, D). Cardinal tooth 3b is at least weakly developed in the Myoconchidae, but 4b is absent, except possibly for obscure traces in *Stutchburia* (fig. 2D). Cardinal teeth characteristically are lacking in left valves of *Rimmyjimina* and *Myoconcha*.

It is probable that the Paleozoic Modiolopsidae gave rise to the Carditacea and primitive lucinoids of the middle and late Paleozoic. This conclusion, of course, is provisional and remains to be documented by means of intermediate morphological stages not yet available. At least two families emerged from the Modiolopsidae, the Myoconchidae and Pleurophoridae. The suggested taxonomic distribution of these forms is as follows:

Superfamily uncertain

Family Modiolopsidae Fischer, 1887

Modiolopsis Hall, 1847

Modiomorpha Hall, 1869

Redonia Rouault, 1851

Modiolodon Ulrich, 1894

Modiodesma Ulrich, 1924

Superfamily Carditacea

Family Myoconchidae Newell, new family

Myoconcha Sowerby, 1824 (= *Labayaphorus* Licharew, 1939)

Stutchburia Etheridge, Jr., 1900

Subgenus *Netchajewia* Jakolew, 1925 (= ? *Rimmyjimina* Chronic, 1952)

Family Pleurophoridae Dall, 1900 (= *Kalenteridae* Marwick, 1953)

Permophorus Chavan, 1954 (= *Pleurophorus* King, 1848, *non* Mulsant, 1842; ? *Pleurophorella* Girty, 1904; ? *Pleurophorina* Licharew, 1925)

Kalentera Marwick, 1953
Triaphorus Marwick, 1953
Celtoides Newell, new genus

SYSTEMATIC DESCRIPTIONS
ORDER HETERODONTA NEUMAYR
SUPERFAMILY CARDITACEA MENKE
MYOCONCHIDAE NEWELL, NEW FAMILY

DIAGNOSIS: Elongate, more or less anisomyarian shells of modioloid aspect with opisthodontic external ligament held on strong nymphs; anterior adductor reënforced behind by a myophoric buttress which bears the impression of a pedal retractor muscle at the dorsal extremity; one well-defined postero-lateral tooth (PII) in left valve separated from hinge margin by a linear socket; one weaker postero-lateral (PI), less commonly a second (PIII) in the right valve; one cardinal tooth (3b) in the right valve and another (4b) may or may not develop in the left valve.

KNOWN RANGE: Cosmopolitan in the Permian (possibly Pennsylvanian) and Mesozoic.

DISCUSSION: The nature of the ligament, the nymphs, and the dentition are quite unlike those of the Mytilacea with which these shells are commonly classed. On the other hand, they are quite similar to those of the Pleurophoridae, from which they differ mainly in the lack of a cardinal tooth equivalent to number 2. The myophoric buttress is somewhat less pronounced in adult *Myoconcha*, the shells of which are heavy, but other genera of the family resemble the Pleurophoridae and Modiolopsidae in the development of this structure.

Very probably the Myoconchidae were derived from the Pleurophoridae, which in turn originated in the Modiolopsidae. By analogy with the mytilaceans, in which there is strong correlation between attachment and reduction of the anterior part of the body, the members of these families were probably byssate.

GENUS *MYOCONCHA* SOWERBY, 1824¹

Figure 2A, B

GENOTYPE: *Myoconcha crassa* Sowerby, 1824, by monotypy, Jurassic. Subjective synonym: *Labayaphorus* Licharew, 1939; genotype by monotypy, *L. magnus* Licharew, 1939, Permian.

DISCUSSION: The possession of well-developed ligament nymphs and

¹ I am indebted to Dr. L. R. Cox for pencil sketches of *Myoconcha crassa* from which figure 2A was prepared.

a weak postero-lateral tooth in the left valve behind (instead of beneath) the ligament distinguishes this genus from the Modiolopsidae. Dechaseaux (1952, p. 321) notes that the shell is not nacreous.

The genotype (fig. 2A) is from the middle Jurassic of England, but similar forms occur sporadically from the Permian to the Cretaceous. Permian species here referred to *Stutchburia* have been classed with *Myoconcha* by many students, but Licharew (1939) has introduced the name *Labayaphorus* (fig. 2B) for a form that is hardly distinguishable from *Myoconcha* of the *crassa* type.

The shells of mature *Myoconcha* are relatively large and heavy, and the myophoric buttress is low. Otherwise, the genus is characterized by the essentially terminal position of the beaks, and by a single, elongate, heavy cardinal tooth in the right valve.

KNOWN RANGE OF THE GENUS: Mid-Permian (Artinskian) to Cretaceous, inclusive.

GENUS *STUTCHBURIA* ETHERIDGE, JR., 1900

Figures 2C, D, 3A

GENOTYPE: *Orthonota? costata* Morris, 1845, by original designation. Permian (upper Marine series) of southeastern Australia.

DIAGNOSIS: Shell modioliform, characterized by a lunule and escutcheon and by poor development of cardinal teeth 2 and 3b, both of which are obsolescent (fig. 2D); lateral teeth PI and PIII poorly developed, but PII is clearly defined; ornamentation lacking or limited to the area behind the pedal sulcus and consisting of fine to moderately coarse ribs.

RANGE: Cosmopolitan in marine rocks of Artinskian-Kazanian age.

SUBGENUS *STUTCHBURIA* (*STUTCHBURIA*)¹

Figure 3A

DIAGNOSIS: Large, subquadrate shells ornamented by coarse ribs.

RANGE: Rocks of Artinskian age, southeastern Australia.

SUBGENUS *NETSCHAJEWIA* JAKOLEW, 1925

Figure 2C, D

SUBGENOTYPE: *Mytilus pallasii* Verneuil, 1845 (= *Pleurophorus modioliformis* King, 1884), by subsequent designation by Newell, 1955. Subjective synonym(?): *Rimmyjimina* Chronic, 1952; genotype, *R. arcula* Chronic, 1952, by original designation.

¹ Mr. H. O. Fletcher, of the Australian Museum, made it possible for me to study the specimen shown as figure 3A.

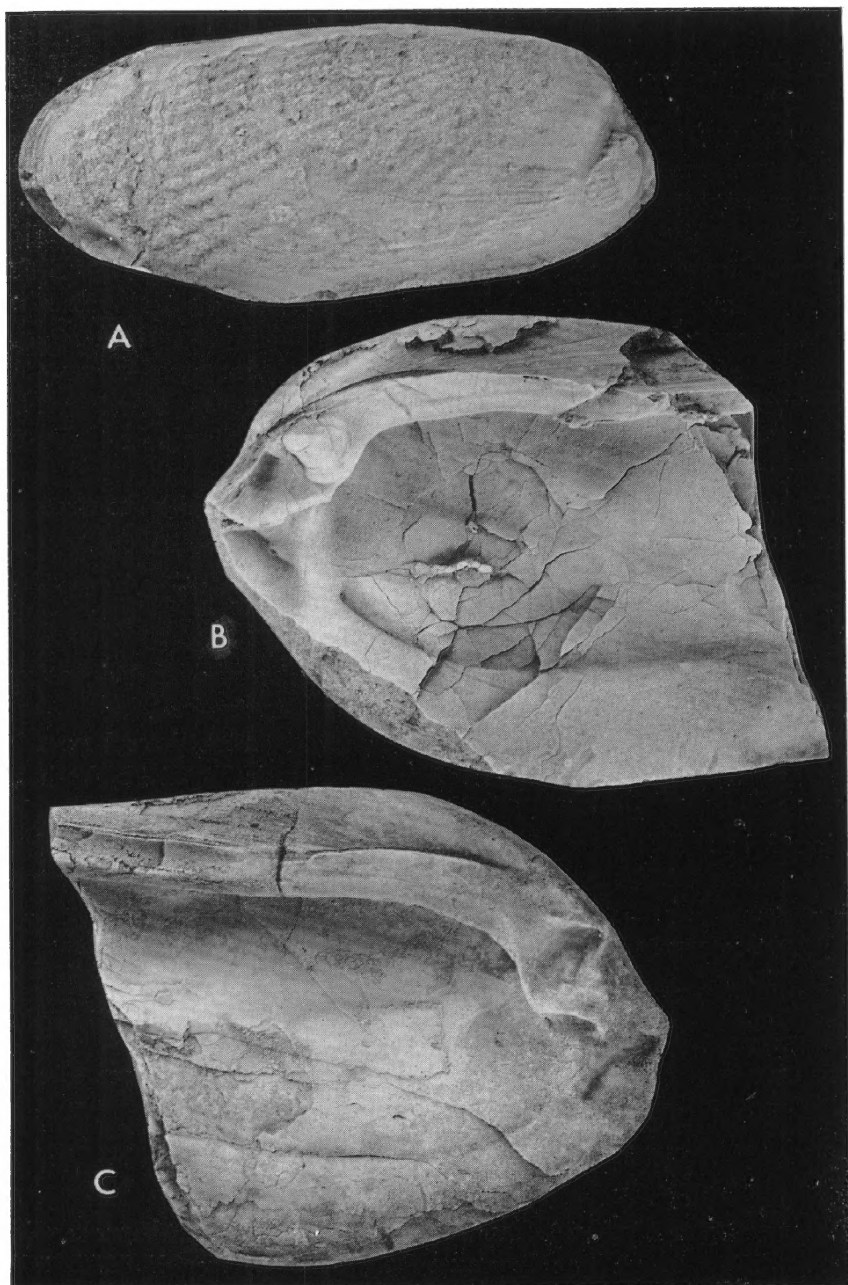


FIG. 3. Permian carditaceans. A. *Stutchburia costata* (Morris), internal mold, upper Marine series, Permian, Kioloa, New South Wales, Australian Museum No. F.19164, $\times 1$. B, C. *Celtoides unioniformis* Newell, new genus and new species, Permian, Wyoming, A.M.N.H. Nos. 28046:1, 28046:2, paratypes, $\times 1$.

DIAGNOSIS: Shells strongly anisomyarian, somewhat attenuate anteriorly, with mytiloid lateral profile; ornamented by fine radial ribs, or smooth.

RANGE: Europe, Asia, North America, Permian (Artinskian to Kazanian).

DISCUSSION: I am uncertain about the validity of *Rimmyjimina* (fig. 2C) which was founded on very small specimens which somewhat resemble *Netschajewia* and may be juveniles of that genus. *Rimmyjimina* was described from the Kaibab limestone of mid-Permian (Leonardian) age; therefore it was contemporaneous with characteristic species of *Netschajewia*. Further discoveries at the original locality of the genotype of *Rimmyjimina* are needed for adequate evaluation.

There is no evident advantage in distinguishing between the smooth and costate shells as separate generic taxa. They intergrade in some of the Permian faunules in western Texas where they are found in mutual association.

FAMILY PLEUROPHORIDAE DALL, 1900 (=KALENTERIDAE
MARWICK, 1953)

GENUS *PERMOPHORUS* CHAVAN, 1954

GENOTYPE: *Arca costata* Brown, 1841, Permian, by monotypy for the preoccupied *Pleurophorus* King, 1844, not *Pleurophorus* Mulsant, 1842. Chavan (1954) has introduced *Permophorus* to replace the junior homonym. Subjective synonyms(?): *Pleurophorella* Girty, 1904; genotype by original designation, *P. papillosa* Girty, 1904, upper Pennsylvanian; *Pleurophorina* Licharew, 1925; genotype by monotypy, *Pleurophorus simplex* Keyserling, 1846 (invalid emendation of *Modiola simpla* Keyserling, 1846), Permian.

DIAGNOSIS: Shell equivalve, elongate, subquadrate or tapering slightly towards the posterior, beaks situated very slightly behind the anterior extremity; dorsal border broadly arched, ventral border nearly straight, but usually slightly indented at a broad and shallow sulcus that extends from the umbones to a place just anterior to the middle of the ventral margin, front and rear ends of the shell rounded; surface nearly smooth, or ornamented behind the pedal sulcus by a few costellae, the anterior part of the shell being marked in some species by radial rows of fine papillae arranged in quincunx, lunule and escutcheon well developed, ligament opisthodontic and parivincular, supported by well-defined nymphs which are limited to the anterior one-fourth of the dorsal margin; anterior adductor strengthened behind by a supporting buttress; dentition consisting usually of one postero-lateral tooth (PIII) in

the right valve along the shell margin which passes over a single lateral (PII) of the left valve; one cardinal tooth in each valve, that of the right (3b) passing above that of the left (2) valve; rarely, there is an additional poorly developed, inner, postero-lateral tooth (PI) and an outer cardinal (4b) in left valves of a few individuals (fig. 2E).

RANGE: Mississippian?-Permian, cosmopolitan.

DISCUSSION: King founded *Pleurophorus* without diagnosis by reference to the type species. Later he described and figured shells with two prominent cardinal teeth in each valve and a marginal lateral tooth in the left valve (King, 1850). Böhm (1914) was unable to verify King's interpretation of the hinge from topotype specimens, and he concluded that King was in error. Newell (1940) independently arrived at the same conclusion and accepted Böhm's interpretation of the characters of the type species of *Pleurophorus*. Chavan (1954) has shown that the hinge is carditacean not cyprinacean, as believed by many students, and he gives the cardinal formula: 2, (4b), PII,—, (3a), 3b, PIII.

I have examined a large series of well-preserved specimens of *Permophorus* from the southwestern United States and have not been able to confirm the existence of tooth 3a. A survey of the literature (excepting King's 1850 work referred to above) fails to indicate that this tooth is developed in any known representative of the genus. The dental formula for the Permian species that I have examined, especially *Permophorus albequus* (Beede), is as follows: 2, (4b) PII,—, 3b, (PI), PIII.

The genus *Pleurophorina* Licharew, 1925, from the Russian Permian closely resembles *Permophorus*. It is supposed to be distinguished, however, by the lack of cardinal tooth number 2. However, Licharew's casts of the hinge do not convincingly document this feature (Licharew, 1925, pl. 1, figs. 1, 2). If Licharew's *Pleurophorina simplex* (Keyserling) does indeed have a hinge essentially like that of *Permophorus costatus* (Brown), then the name *Pleurophorina* would take precedence over *Permophorus*.

Additional uncertainty about the status of *Permophorus* is introduced by the possibility that *Pleurophorella* Girty, 1904, may be a subjective synonym of *Permophorus* in the broad sense. *Pleurophorella* is a papillose, non-costate shell from the upper Pennsylvanian. Externally it is quite similar to non-costate examples of *Permophorus* from the Pennsylvanian and Permian of the western United States. Unfortunately, the internal characters of the hinge are as yet unknown.

CELTOIDES NEWELL, NEW GENUS

GENOTYPE: *Celtoides unioniformis* Newell, new species, Permian.



FIG. 4. Permian carditacean. *Celtoides unioniformis* Newell, new genus and new species, Permian, Wyoming, A.M.N.H. No. 28046, holotype, $\times 1$.

DIAGNOSIS: Robust, thick-shelled, unornamented pleurophorids, subacute anteriorly, somewhat attenuate and laterally compressed posteriorly; pedal region undifferentiated; lunule small, escutcheon broad; dental formula: 2, (4b), PII, —, 3b, PIII; the cardinal tooth 2 is appreciably less prominent than 3b.

DISTRIBUTION: Marine Permian (Guadalupian), Wyoming, United States.

DISCUSSION: The large shell size and general expression of the type species recall certain species of unionids. Consequently, I at first thought that it might be a Paleozoic forbear of the fresh-water mussels. The resemblance, however, is only superficial. The ligament nymphs and dentition are heterodont characters similar to those of *Permophorus*.

***Celtoides unioniformis* Newell, new species**

Figures 3B, C, 4

DIAGNOSIS: Shell wall thick, 5 mm. more or less over the middle of a mature valve; shell large, about 12.5 cm. long in the holotype, twice as long as high. Dorsal margin concave, ventral margin evenly convex, without pedal sinus; anterior margin slightly acuminate, extended appreciably in front of the beaks, posterior narrowly rounded, probably with a slight gape.

DISCUSSION: The dentition of *C. unioniformis* is closely similar to that of the shells of *Permophorus* that I have examined. There are, however, minor distinguishing features. In *Permophorus*, tooth 2 tends to be larger and more prominent than 3b, but the reverse is the case in *Celtoides*. The ventral surface of tooth 3b is impressed by a radial furrow (fig. 3B), a feature unknown in *Permophorus*. Papillae such as those of *Permophorus* are not visible on the exterior of the shells of *Celtoides*. However, the material is silicified and the quality of preservation is fair, so that the original character of the surface is not absolutely certain. In addition to the figured specimens, there are fragments of four valves.

DISTRIBUTION: Collected from dolomitic limestone in association with silicified large *Bellerophon* sp. Occurs sparsely in the Franson (middle) limestone member of the Park City formation, equivalent to the Rex chert of the Phosphoria formation (McKelvey *et al.*, 1956) in the region about DuBois, Wyoming. The types were collected at a roadside exposure, entrance to Torrey Lake, 8 miles southeast of DuBois, Wyoming (A.M.N.H. locality 342).

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